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Distribution, biology and habitat of the rare European osmiine bee species *Osmia* (*Melanosmia*) *pilicornis* (Hymenoptera, Megachilidae, Osmiini)

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Abstract

Osmia pilicornis is distributed from western temperate Europe to western Siberia, where it exclusively occurs in open-structured, mesophilous and mainly deciduous woodland below 1000 m a.s.l. In Central Europe, its peak activity ranges from the last third of March to the first third of June. Due to its rarity and its low population densities over most of its range, the biology of *O. pilicornis* was only fragmentarily known. The discovery of six nests in the course of the present study revealed that females of *O. pilicornis* have a unique nesting behaviour among the osmiine bees: they gnaw their nests in dead wood with the aid of their strong mandibles, which have a peculiar chisel-like shape hypothesized to be an adaptation to the species' specialized nesting behaviour. All six nests were in dead fallen branches of different tree and shrub species and of varying wood hardness. The nesting branches had a diameter of 1.5–6.1 cm, lay on sun-exposed ground and were largely hidden under vegetation. The nests contained one to three linearly arranged brood cells. Both cell partitions and nest plug were built from chewed leaves harvested from *Fragaria vesca*. *Osmia pilicornis* was identified as a new host of the chrysidid wasp *Chrysura hirsuta*, and the ichneumonid wasp *Hoplocryptus confector* developed in its nests. Microscopical analysis of scopal pollen loads of collected females revealed that pollen is mainly collected from three plant taxa, i.e. *Pulmonaria* (Boraginaceae), Fabaceae (e.g. *Lathyrus*, *Vicia*) and Lamiaceae (e.g. *Ajuga*, *Glechoma*). On flowers

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of *Pulmonaria*, which is the most important pollen host over most of the species' range, the females use specialized bristles on their proboscis to brush pollen out of the narrow corolla tube, they almost exclusively exploit pollen-rich flowers in the early red stage and they often steal pollen from still closed flowers by forcefully opening buds. On their search for females, males of *O. pilicornis* patrol flowers of *Pulmonaria* in a rapid flight regularly interrupted by short resting periods on the ground. Females are grasped for copulation both during flower visits and in flight between the flowers. The wide spectrum of semi-open mesophilous woodland types colonized by *O. pilicornis* suggests that dead fallen branches and a rich spring flora in combination with a rather warm but not xeric microclimate are the only requisites needed by the species. As the great majority of woodland habitats currently occupied by *O. pilicornis* in Central Europe owe their origin to human forest use, the recent decline of *O. pilicornis* in many regions of Europe may have been caused by changes in woodland management practices leading to closed and dark forests not suitable as habitats for this specialized bee species.

Keywords
Apiformes, *Chrysura hirsuta*, dead wood, *Hoplocryptus confector*, *Pulmonaria*, nesting behaviour, open-structured woodland

Introduction

Osmia pilicornis Smith is a member of the large holarctic subgenus *Melanosmia* represented by 12 species in Europe (Müller 2016). Most of the European *Melanosmia* species are adapted to colder climates and typically occur in mountainous habitats, often exhibiting an alpine, boreoalpine or boreal distribution (Tkalců 1983, Rightmyer et al. 2010, Müller 2016). *Osmia pilicornis*, whose distribution area ranges from western over central and eastern temperate Europe to western Siberia, belongs to those few European *Melanosmia* species, which are restricted to lower elevations. Its early appearance in spring and its exclusive occurrence in mainly mesophilous woodland habitats, however, suggests a moderate preference for colder climates revealing its affiliation to *Melanosmia*.

Osmia pilicornis is regarded as a rare bee species over most of its range (Westrich 1989, Amiet et al. 2004, Westrich et al. 2008, Falk and Lewington 2015). In several European countries, it is listed on regional or national red lists since its populations have declined in many regions in recent decades (Amiet 1994, Winter 1994, Dathe and Saure 2000, Saure 2005, Westrich et al. 2000, 2008, Van der Smissen 2001, Theunert 2002, Mandery et al. 2003, Burger et al. 2004, Burger 2005, Straka 2005, Tischendorf et al. 2009, Esser et al. 2010, Earwaker 2012). Changes in woodland management practices are assumed to be a major cause of its decline, resulting in a lack of suitable food plants and nesting sites (Earwaker 2012, 2014). Given the threatened status of *O. pilicornis* in parts of its European range, knowledge of the species' requirements for nesting sites, host plants and habitat characteristics is needed to aid in its conservation.

The preference of *Osmia pilicornis* for the flowers of *Pulmonaria* (Boraginaceae) as pollen hosts has been known for a long time (Stoeckhert 1933, Westrich 1989, Müller

1995, Amiet et al. 2004, Ebmer 2010), as has the presence of specialized bristles on the female proboscis, which are used to brush pollen out of the narrow *Pulmonaria* corolla tubes (Müller 1995). In contrast, the nesting biology of *O. pilicornis* is virtually unknown. While masticated leaves ("leaf pulp") have recently been identified as nest building material (Westrich 2010), the nesting sites are still enigmatic. Depending on the author, *O. pilicornis* was assumed to burrow in stony ground (Wallis 1886), to nest in empty snail shells (Friese 1911, Banaszak and Romasenko 2001), to gnaw burrows in dead wood (Wallis 1886, Perkins 1891), to nest in old tree stumps or branches lying on the ground (Blüthgen 1919, Stoeckhert 1933, Chambers 1949), to build brood cells under loose bark (Amiet et al. 2004) or to colonize preexisting insect borings in dead wood (Earwaker 2014, Falk and Lewington 2015). While the assumption that *O. pilicornis* nests in the ground or in snail shells appears to be unlikely and is probably due to misidentifications with similar species, all the other literature records clearly suggest dead wood as nesting substrate. However, as no nests in dead wood have ever been described in detail, the question remains open whether the females of *O. pilicornis* excavate their own burrows, build their brood cells under loose bark or nest in insect borings.

In the present publication, we describe nesting site, nest architecture and nesting behaviour of *Osmia pilicornis* based on the recent discovery of several nests in Germany and Austria. In addition, we report on a hitherto unknown host-parasitoid relationship between *O. pilicornis* and a chrysidid wasp, investigate host-plant spectrum and flower-visiting behaviour based on both analysis of female pollen loads and field observations and describe the mating strategies of the males. Furthermore, we present a comprehensive distribution map and characterize phenology and habitat of *O. pilicornis* focussing on Central Europe.

Methods

To elucidate the distribution of *Osmia pilicornis*, we conducted a comprehensive literature study, gathered unpublished records from European entomological collections and retrieved distributional data from several public databases. Numerous additional records were provided by bee researchers all over Europe. For details see Acknowledgments and Suppl. material 1, which contains a complete list of all distributional data.

To evaluate the phenology of *Osmia pilicornis* in Central Europe, all records were considered that could be assigned to sex and an exact date. Central Europe is defined here as the area that comprises Austria, Czech Republic, Germany, Hungary, Poland, Switzerland, Slovakia and Slovenia.

Field work was mainly conducted in southern Germany near Crailsheim (Baden-Württemberg) from 12 April to 15 May 2015 and from 10 April to 30 May 2016. Additional study sites were near Ernstbrunn (Niederösterreich) in northeastern Austria and near Flaach (Zürich) and Schaffhausen (Schaffhausen) in northern Switzerland, where field work was done in April and May 2016. The four study sites differed in the *Pulmonaria* species available for *Osmia pilicornis*: the first contained only *P. mollis*

Wulfen ex Hornemann, the second and third only *P. officinalis* Linné and the fourth only *P. obscura* Dumortier.

To uncover the pollen-host preferences of *Osmia pilicornis*, the scopal pollen contents of 52 female specimens collected at 49 different localities in Austria (n=18), Germany (n=16), Switzerland (n=13) and the Czech Republic (n=5) from 1903 to 2013 as well as the pollen provisions of three brood cells originating from two nests were microscopically analysed following the method of Müller (2015).

Flowers of *Pulmonaria* change their colour from red to blue during anthesis, which lasts about five to eight days (Oberrath et al. 1995, Oberrath and Böhning-Gaese 1999). This colour change, which takes place approximately in the middle of anthesis, is caused only by aging and thus independent of pollination (Süssenguth 1936, Oberrath et al. 1995). To investigate whether females of *Osmia pilicornis* discriminate between *Pulmonaria* flowers in the early red and the late blue stage, we counted flower visits on red and blue flowers of *P. mollis* on a plot of 15×15 m on six days during ten intervals each lasting from 0.5 to 2.5 h. Counting occurred during two periods from 7 to 10 May 2016 and from 20 to 21 May 2016. After each interval, the total number of red and blue flowers of all plant individuals that were visited by the female bees was determined. To compare the nectar quantity contained in *Pulmonaria* flowers of the red and the blue stage, we determined the nectar amount in 33 red and 33 blue flowers of *P. mollis* with 10 µl microcapillaries. The flowers for nectar quantification were collected on the same day in early morning before the onset of insect activity. To compare the pollen quantity contained in *Pulmonaria* flowers of the red and the blue stage, we determined the pollen amount in 20 red and 20 blue flowers each of *P. obscura* and *P. officinalis*. As a proxy for the pollen amount we estimated the proportion of the thecal surface that was covered by pollen (to the nearest 10%) separately for each of the ten thecae of a flower and averaged the ten percentages to get an average degree of thecal pollen coverage for each flower. For both *Pulmonaria* species, the flowers were collected on the same day between 11 and 12 am, stored in open eppendorf tubes and slit the following morning for pollen quantification. To investigate the proportion of already dehisced vs. still closed anthers in flowers of the late bud stage, we opened 20 buds of *P. officinalis*.

Pulmonaria is distylous with two floral morphs, which occur on separate plants and differ in the relative height of anthers and stigma and the size of the pollen grains (Olsen 1979; Fig. 27, 28). The ratio of plants with longistylous and brevistylous flowers often deviates from 1:1 within the same population and may vary between different populations (Brys et al. 2008). To investigate whether females of *Osmia pilicornis* prefer one of the two floral morphs, the morph of each *P. mollis* plant growing on the 15×15 m study plot was determined after the female flower-visiting behaviour was recorded (see above).

To take photos, video sequences and photomicrographs, we used a Canon EOS 70D with 150 mm macro lens and macro flashlights, a Camcorder Panasonic HC V777 and a digital microscope Keyence VHX-2000, respectively. For statistical analyses, SPSS 22.0.0.2 for Macintosh OS X (SPSS Inc., Chicago, IL, USA) was used.

Results

Distribution

Osmia pilicornis occurs from western, central and eastern temperate Europe eastwards to the Kemerovo region in western Siberia (Fig. 1). It inhabits a rather narrow belt between 44.5° and 62.5° northern latitude, extending from 3.5° western to 87.5° eastern longitude (Table 1). It is distributed from sea level up to about 950 m a.s.l., with the highest records all lying below 1000 m a.s.l. It has been recorded so far from (west to east) southern Great Britain, northern France, Belgium, western and northern Switzerland, Luxembourg, Germany, Denmark, Austria, southern Sweden, Czech Republic, Slovenia, Hungary, Slovakia, Poland, Romania, Lithuania, southern Finland, Latvia, Belarus, Ukraine and Russia (southern North-West district, Central district, Wolga district, southern Ural district, southwestern Siberia district). Wu (2006) reports *O. pilicornis* from the Taihang mountains in Hebei province in northeastern China, which is about 2600 km to the east of the easternmost records of *O. pilicornis* in western Siberia. This record appears to be doubtful and needs verification as already demanded by Ebmer (2010).

Phenology in Central Europe

Osmia pilicornis emerges early in spring (Fig. 2). Its appearance coincides with that of other early bee species, such as *Andrena bicolor* Fabricius, *Anthophora plumipes* (Pallas), *Eucera nigrescens* Pérez, *Osmia bicolor* (Schrank) and *Osmia bicornis* (Linné). In Central Europe, the earliest records are 22 February for males and 18 March for females. Males have their peak activity from the last third of March to the first third of May and occasionally fly until mid May. The latest male record in Central Europe is 17 May. Females have their peak activity from the first third of April to the first third of June and occasionally fly until the end of July. The latest female record in Central Europe is 4 August. While the males emerge only a few days before the females, their flight period is roughly one month shorter, indicating that the females have a distinctly longer average life span than the males.

Nesting biology

Nesting site

Six nests of *Osmia pilicornis* were discovered in 2015 and 2016. Five nests were found on a 0.8 ha large and about five years old clear-cutting in a former spruce plantation with numerous plants of *Pulmonaria mollis* near Crailsheim (Baden-Württemberg) in southern Germany (10.11°E 49.18°N, 450 m a.s.l., Fig. 42). One nest was detected in a recently thinned, very light and oak-dominated deciduous forest with large stands

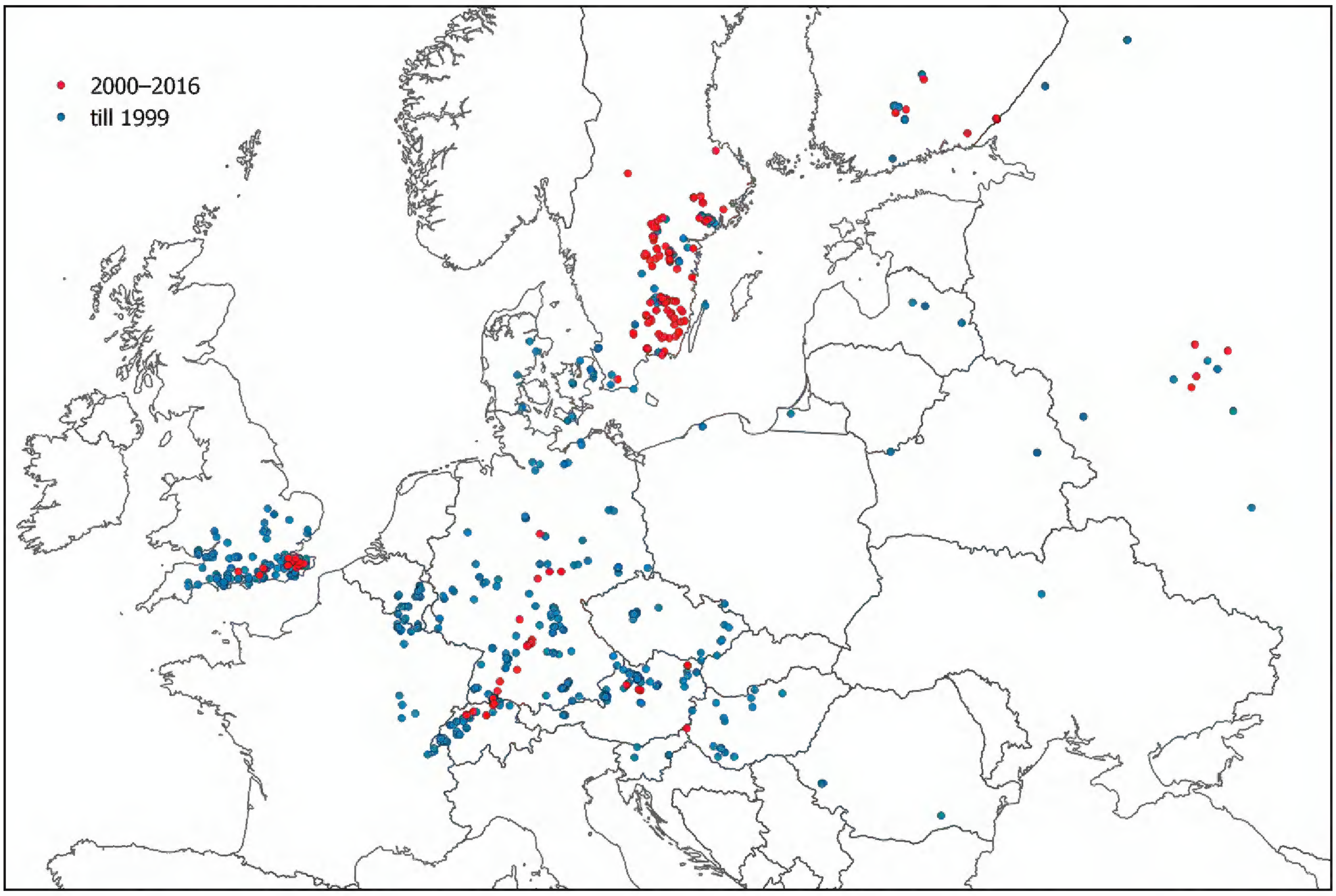


Figure 1. Distribution of *Osmia pilicornis*. Records east of the Ural mountains are not shown.

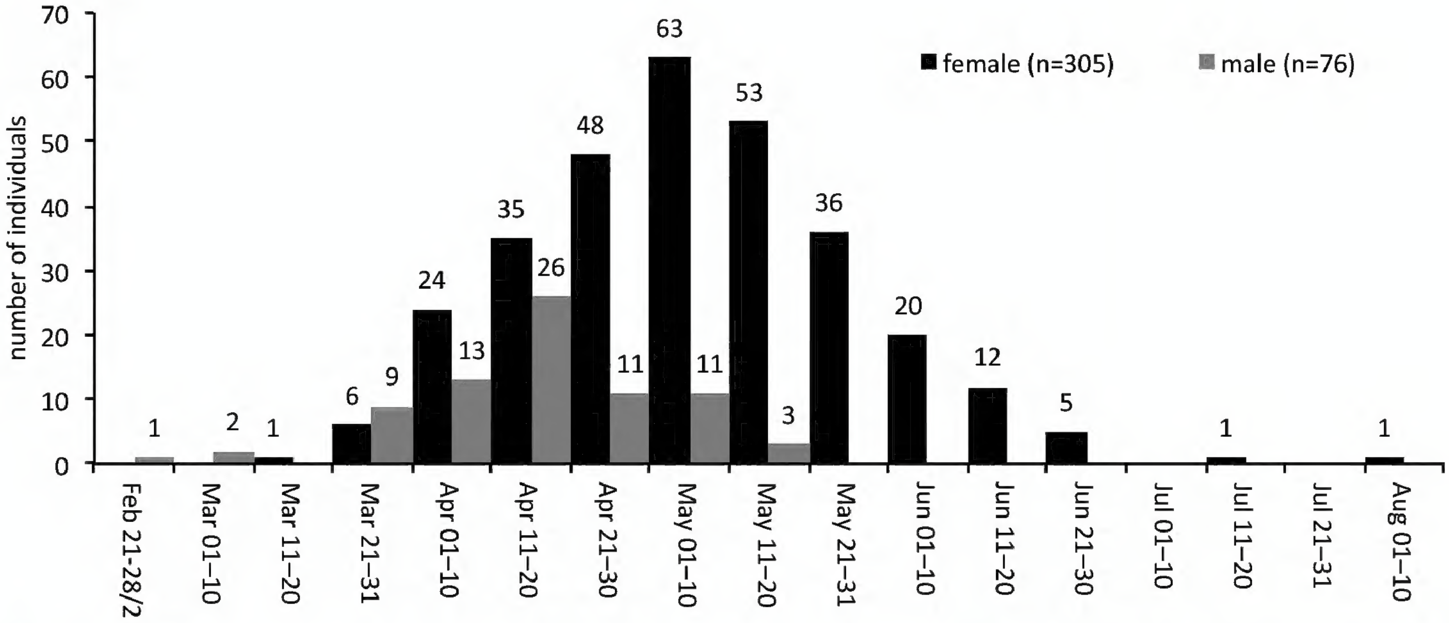


Figure 2. Phenology of *Osmia pilicornis* in Central Europe. Central Europe is defined here to comprise Austria, Czech Republic, Germany, Hungary, Poland, Switzerland, Slovakia and Slovenia.

of *Pulmonaria officinalis* near Ernstbrunn (Niederösterreich) in northeastern Austria (16.35°E 48.59°N, 330 m a.s.l., Fig. 44).

All six nests were burrows excavated by the female bees in dead branches lying on sun-exposed ground (Table 2, Figs 3–11). One branch contained two separate nests built by two females (nesting site 1), another branch also contained two nests, which, however, were probably constructed by the same female (nesting site 3), and

Table 1. Southern-, northern- western- and easternmost as well as highest records of *Osmia pilicornis*. Only one record per country is given for the southernmost, northernmost and highest records.

	Locality	Source
southernmost records	Romania, Călăraşi, Fundulea, 26.511E, 44.464N	Aftene (1995)
	Slovenia, Črni Vrh, Pasja ravan, 14.229E, 46.098N	A. Gogala (personal communication)
	Hungary, Baranya, Mecsek, Remete-árok, 18.217E, 46.118N	M. Sarospataki (personal communication)
	Switzerland, Genève, Dardagny, 5.949E, 46.177N	database of Centre Suisse de Cartographie de la Faune (CSCF)
	France, Côte-d'Or, Reulle-Vergy, 4.905E, 47.181N	M. Aubert and G. Le Goff (personal communication)
northernmost records	Russia, Karelia, Kondopozhskiy rayon, Tivdiya, 33.961E, 62.561N	J. Paukkunen (personal communication)
	Finland, Western Finland, Korpilahti, Korospohja, 25.732E, 61.917N	J. Paukkunen (personal communication)
	Sweden, Uppsala, Brändäng, 17.482E, 60.447N	A. Nilsson (personal communication)
westernmost records	United Kingdom, Devon, 3.630W, 50.743N	database of Global Biodiversity Information Facility (GBIF)
	United Kingdom, Wales, Castell Coch, 3.247W, 51.534N	database of Global Biodiversity Information Facility (GBIF)
easternmost records	Russia, Kemorovo, Tashtagol district, Kaz, 87.542E, 53.108N	T. Levchenko (personal communication)
	Russia, Kemerovo, Karakan Mountains, 86.932E, 54.364N	T. Levchenko (personal communication)
highest records	Slovenia, Črni Vrh, Pasja ravan, 970m a.s.l.	A. Gogala (personal communication)
	Germany, Baden-Württemberg, Swabian Jura, Obernheim, 950m a.s.l.	Westrich (2010, personal communication)
	Switzerland, Bern, La Neuveville, Neuve Métairie, 860m a.s.l.	database of Centre Suisse de Cartographie de la Faune (CSCF)
	Austria, Salzburg, Hinterwinkl near Ebenau, 700m a.s.l.	M. Schwarz (personal communication)

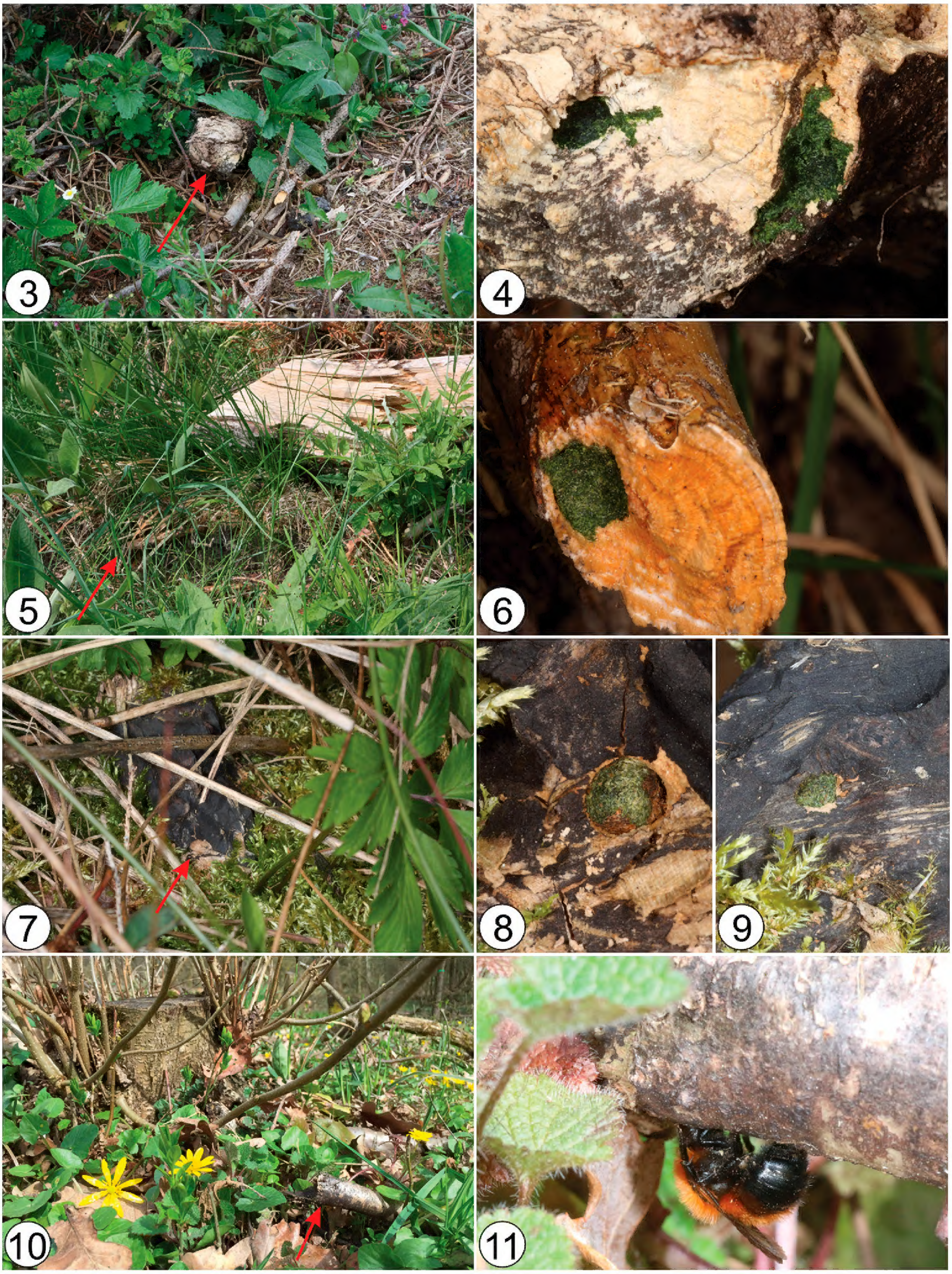
two branches contained one nest each (nesting sites 2 and 4). The branches selected as nesting sites had a length of 7.5–85 cm and a diameter of 1.5–6.1 cm, were largely hidden under vegetation and belonged to four different tree or shrub species. The females started to gnaw the nest burrows either in the apical area of branch fracture (n=4), on the side of the branch (n=1) or on the underside of the branch about 10 cm above ground (n=1). The nest entrances were exposed to south-southwest (n=3), southeast (n=1) or northeast (n=1). The hardness of the nesting wood varied from very hard (n=2) and moderately hard (n=1) to soft (n=1).

Nest architecture

The nests of *Osmia pilicornis* were composed of i) a burrow tunelled out by the female bee, ii) a varying number of brood cells each delimited towards the nest entrance by a

Table 2. Characteristics of six nests of *Osmia pilicornis* discovered in Germany (nesting sites 1–3) and Austria (nesting site 4). The hardness of the wood is indicated by the following categories: very hard = impossible to scratch the wood with the fingernail; moderately hard = possible to scratch the wood with the fingernail, but impossible to burrow a hole with the finger; soft = possible to burrow a hole with the finger.

Nesting site no	Species of branch	Length and diameter of branch	Hardness of wood	Degree of concealment of branch	Wood infesting fungi	Nest no	Location of nest entrance	Direction of nest entrance	Number of brood cells
1	*Fraxinus excelsior*	85 cm × 6.1 cm	very hard	hidden under vegetation except for the apical 9 cm	*Hypoxylon rubiginosum* (Xylariaceae), *Xylaria hypoxylon* (Xylariaceae), *Phanerochaete* spec. (Phanerochaetaceae)	1	apical area of fracture	SSW	3
						2	apical area of fracture	SSW	2
2	*Picea abies*	18 cm × 1.5 cm	very hard	almost completely hidden under vegetation except for the apicalmost part	Corticiaceae spec.	3	apical area of fracture	SSW	1
3	*Salix* spec.	7.5 cm × 3.5 cm	soft	almost completely hidden under vegetation except for the apicalmost part		4	apical area of fracture	SE	2
						5	side of branch about 3.5cm behind apical area of fracture	NE	1
4	*Corylus avellana*	25 cm × 2.5 cm	moderately hard	hidden under vegetation except for the apical 5 cm		6	underside of branch about 2 cm behind apical area of fracture and 10 cm above ground	-	unknown



Figures 3–11. Nesting sites of *Osmia pilicornis* in dead fallen branches (see Table 2): **3–4** Nesting site 1 with nests 1 and 2 in a branch of *Fraxinus excelsior* **5–6** Nesting site 2 with nest 3 in a branch of *Picea abies* **7–9** Nesting site 3 with nests 4 and 5 in a branch of *Salix* spec. **10–11** Nesting site 4 with nest 6 in a branch of *Corylus avellana*.

cell partition, iii) a (facultative) empty space ("vestibule") of varying length in front of the outermost cell and iv) a nest plug that closed the nest at the front end (Figs 12–14). There was no basal wall that sealed the nest burrow against the rear end.

The excavated burrows consisted of a short entrance part, which was 6–7 mm long and 5–6.4 mm wide, and a main part, which ran in longitudinal direction of the branch and contained the brood cells. The main part deviated from the entrance part by an angle of 90–140°. Depending on the number of brood cells, the total length of the burrows was 1.7–3.2 cm. The burrow and cell walls were neither lined with glandular secretions nor with leaf pulp except for a small area of less than 15 mm^2 in the rearmost brood cell of nest 4, which was covered by a thin layer of leaf pulp. In nest 3, the gnawing female obviously met a preexisting burrow of the cerambycid beetle *Molorchus minor* (Linné) running in longitudinal direction of the branch and adopted it as part of her own burrow by broadening its diameter from 2.8 mm to 5.7 mm (Fig. 13).

The nests contained one (n=2), two (n=2) or three (n=1) linearly arranged brood cells. Brood cell number could not be assessed in one nest as the nesting branch disappeared in the course of the study for unknown reasons. The brood cells had a length of 9.7–12.4 mm and a maximal width of 5.4–6.5 mm. They were widest in the centre and slightly constricted at both ends. The cell partitions were one-layered and had a width of 1–1.25 mm along the burrow wall.

Three out of five nests contained a vestibule between the outermost cell partition and the nest plug measuring 4–6 mm in length. In the other nests, no vestibule was developed; instead, the outermost cell partition was part of the nest plug.

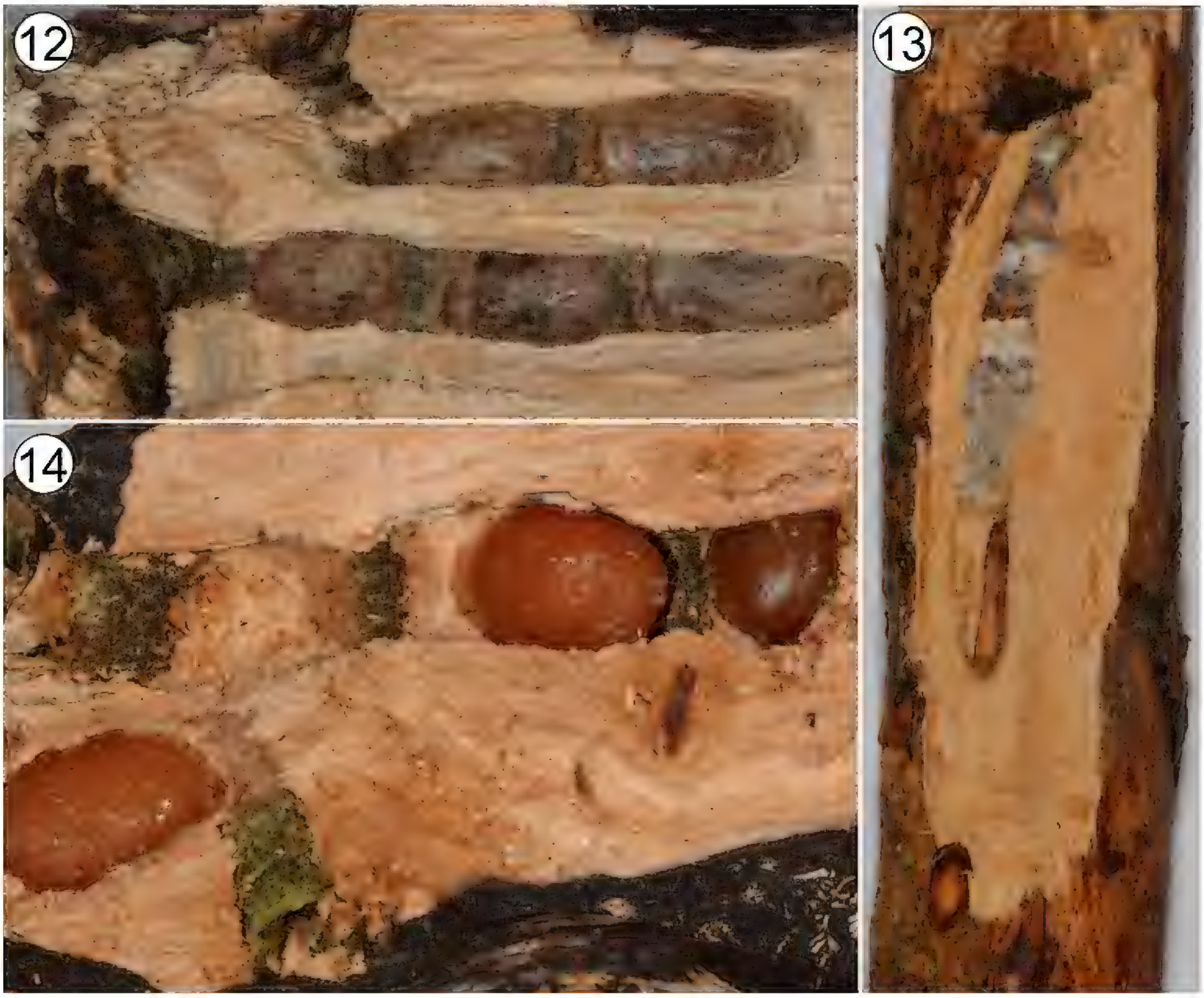
The nest plugs measured 3–7.5 mm in length. They were multi-layered and consisted of 2–4 and 1–2 mm thick walls, which were built immediately behind each other. The nest plugs were flush with the nest entrance (n=3) or recessed by 2.5–3.5 mm (n=2).

Both cell partitions and nest plug exclusively consisted of leaf pulp. At nesting sites 1–3, females of *Osmia pilicornis* were repeatedly observed to collect leaf material from *Fragaria vesca* Linné (Fig. 19).

Female nesting behaviour

The females of *Osmia pilicornis* gnawed their nests in dead wood exclusively with the aid of their mandibles (Figs 15, 16, Suppl. material 2). At nesting site 1, the female was repeatedly observed to burrow for a period of 10–15 sec, before she left the nest for a short circular flight of 1–1.5 m diameter, during which she dropped the carved wood chips that she had held in her mandibles. Occasionally, the female pushed the wood chips with her legs backwards out of the nest. It took about 10 min from the start of carving at the surface of the very hard *Fraxinus* branch until head and mesosoma had disappeared within the substrate, indicating a remarkably high speed of tunneling.

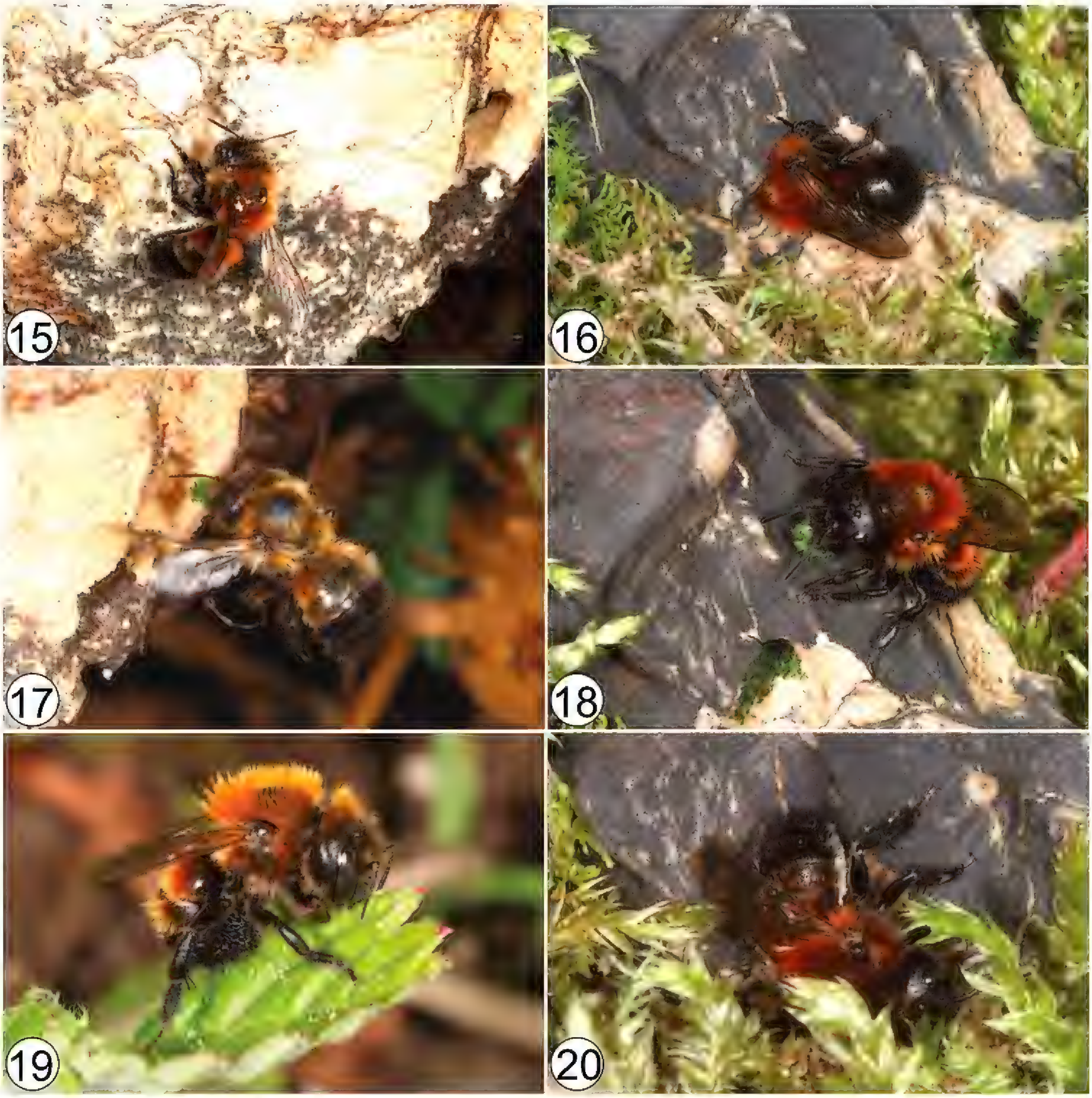
The shape of the female mandible of *Osmia pilicornis* differs from that of closely related *Osmia* (*Melanosmia*) species, such as *O. inermis* or *O. parietina* (Figs 21–26).



Figures 12–14. Opened nests of *Osmia pilicornis* in dead branches (see Table 2): **12** Nests 1 and 2 with three and two brood cells, respectively, each containing a cocoon spun by the *O. pilicornis* larva **13** Nest 3 with one brood cell containing a cocoon spun by the *O. pilicornis* larva; at the bottom a pupa of *Molorchus minor* (Cerambycidae) **14** Nests 4 and 5 with two and one brood cell, respectively, each containing a larval provision; an empty vestibule is present between the outermost cell partition and the nest plug in nest 4, while the cell partition is part of the nest plug in nest 5.

In *O. pilicornis*, the mandible has a much broader and distinctly more inflated base, is relatively shorter, has less diverging margins and is apically only slightly curved inwards giving it a more compact and chisel-shaped appearance. In addition, the uppermost mandibular tooth is more prominent being as large as the medial tooth so that the apices of all mandibular teeth are almost at the same height forming a regular three-toothed apical edge.

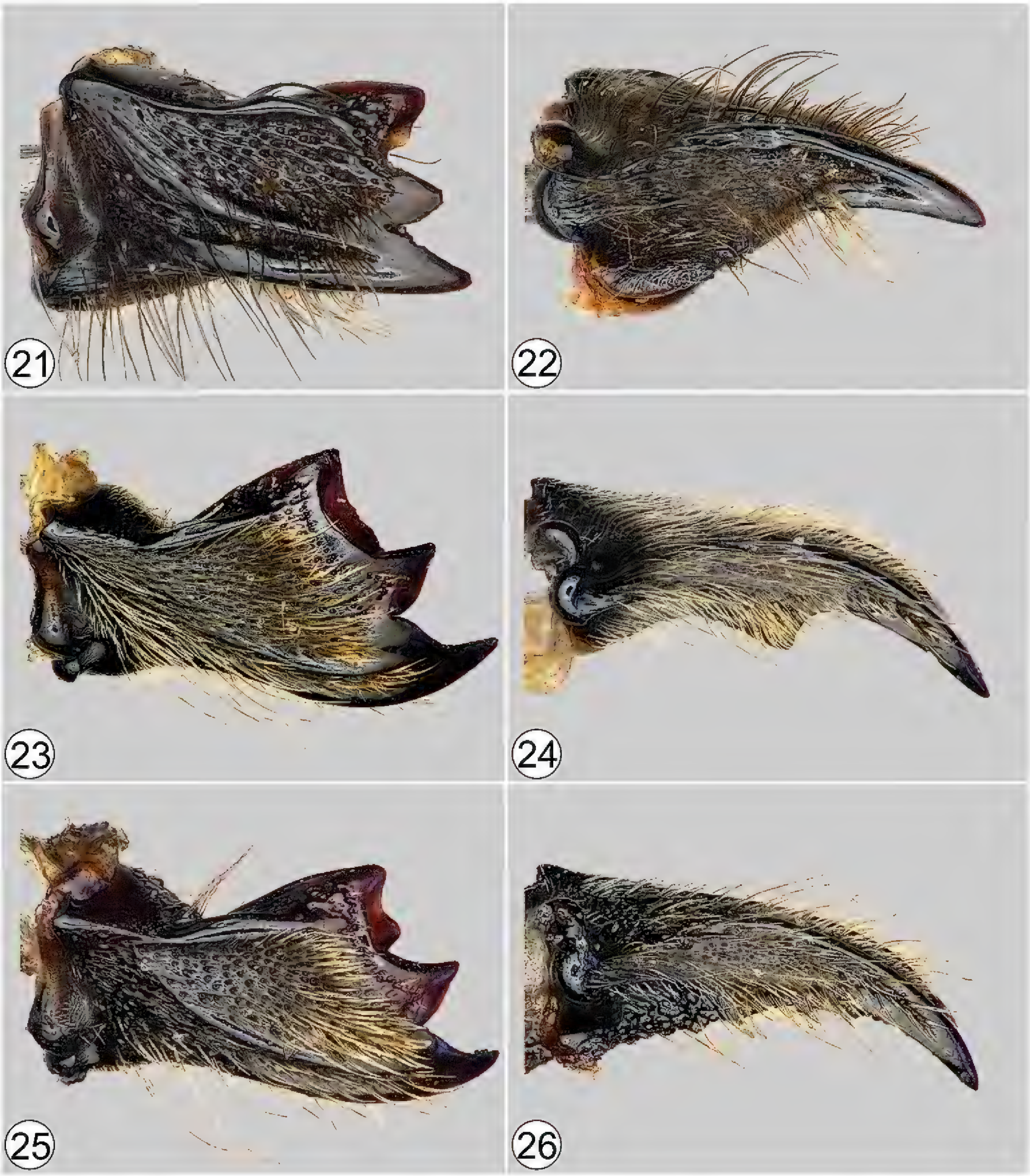
The female of nest 1 needed 25 foraging flights to provision a single brood cell. This female spent 0.6–19.9 min for one provisioning flight (mean 8.7 min, n=25) and remained 10–105 sec within the nest to deposit nectar and pollen (mean 48 sec, n=25). The female of nest 4 returning from a provisioning flight entered the nest head first to regurgitate nectar before she came out, turned around at the nest entrance and entered the nest metasoma first to comb pollen out of the scopa (Fig. 20, Suppl. material 3). The first phase lasted about 25 sec (n=2), suggesting that the regurgitation of nectar



Figures 15–20. Nesting behaviour of *Osmia pilicornis* (see Table 2): **15–16** Females of nests 1 and 4 tunneling out burrows in dead branches **17–18** Females of nests 2 and 4 transporting small leaf fragments of *Fragaria vesca* to build brood cell partitions and nest plug **19** Female harvesting nest-building material on a leaf of *Fragaria vesca* **20** Female of nest 4 returning from a foraging flight with pollen-filled metasomal scopa.

and the deposition of pollen require a similar amount of time. Turning at the nest entrance was not observed at nest 1. Here, there was probably enough space within the burrow allowing the female to turn inside the nest. At nest 1, the last provisioning flight took place at 7:27 pm (temperature 22 °C) and the first provisioning flight the subsequent day at 8:49 am (nesting site in full sunlight), indicating a remarkably long daily activity of more than 10.5 h under favourable conditions.

The females harvested leaf material of *Fragaria vesca* with their mandibles (Fig. 19). They transported it as small leaf fragments rather than as masticated pellets back to



Figures 21–26. Female mandibles of three closely related *Osmia* (*Melanosmia*) species; left=mandible in front view, right=mandible from below: **21–22** *O. pilicornis* **23–24** *O. inermis* **25–26** *O. parietina*. Figures are not to scale.

their nest (Figs 17, 18, Suppl. material 4). As cell partitions and nest plug were built mainly from masticated leaves, the leaf fragments were probably chewed to leaf pulp during their processing inside the nest. The collection of leaf pulp by the female of nest 1 lasted 5–155 sec per flight including flight time (mean 27 sec, n=21) and its processing inside the nest 5–355 sec (mean 75 sec, n=21).

Brood parasites

A female of the chrysidid wasp *Chrysura hirsuta* (Gerstaecker) was observed to visit nest 1 on 11 May 2015 three times in succession (Fig. 37). During the first visit, the wasp lurked at a distance of 2 cm from the nest entrance during 19 min, before she entered the nest headfirst and left it a few seconds later backward. During the second visit, the wasp intruded the nest again headfirst, backed out and immediately entered the nest a second time, but now backward, thereby possibly laying an egg into the brood cell; after about 15 sec she reappeared at the nest entrance and flew away. During the third visit, the wasp was collected for identification. Similarly, females of *C. hirsuta* were repeatedly observed in the close neighbourhood of nest 6 on four days from 2 to 21 April 2016. In contrast to nest 1, however, *C. hirsuta* was not observed to approach or enter the nest.

Five out of the six brood cells of nests 1–3 discovered in 2015 were parasitized, suggesting a high pressure exerted by brood parasites on *Osmia pilicornis*. In all three cells of nest 1, including the cell that was entered by *Chrysura hirsuta* (see above), females of the ichneumonid wasp *Hoplocryptus confector* (Gravenhorst) developed. A female of the same ichneumonid species emerged from the rear cell of nest 2, while the front cell contained inside the larval cocoon of *O. pilicornis* a cocoon with a dead chrysidid wasp larva most probably of *C. hirsuta*. The only unparasitized cell was the single cell of nest 3, in which a male of *O. pilicornis* developed.

As a possible further brood parasite we noticed a single triungulin larva of *Meloe violaceus* Marsham (Meloidae) adhering to the body of a male of *Osmia pilicornis*.

Host plants

Pollen hosts

The microscopical analysis of 52 pollen loads originating from 49 different localities in Central Europe revealed that *Osmia pilicornis* is polylectic harvesting pollen from the flowers of at least eight plant families (Table 3). However, pollen of the three families Boraginaceae, Fabaceae and Lamiaceae strongly dominated constituting 93.5% of the total pollen grain volume. Pollen of all other plant families was recorded in small percentages only. By far the most important pollen host was *Pulmonaria* (Boraginaceae); its pollen represented 58.6% of the total pollen grain volume and was recorded in 35 (67.3%) out of 52 loads, 22 of which were pure *Pulmonaria* pollen loads. The importance of *Pulmonaria* is also revealed by the finding that the larval provisions of three brood cells of nests 4 and 5 exclusively consisted of *Pulmonaria* pollen. The second most important pollen was of the *Lathyrus*-*Vicia*-type (Fabaceae), which unites the morphologically very similar pollen of the closely related genera *Lathyrus* and *Vicia*; this pollen type constituted 14.8% of the total pollen grain volume and was found in 15 (28.8%) loads. The third most important

Table 3. Pollen composition of female pollen loads of *Osmia pilicornis*. n=52 pollen loads from 49 different localities in Austria (n=18), Germany (n=16), Switzerland (n=13) and Czech Republic (n=5).

Plant family	Plant genus/subfamily or pollen type	% pollen grain volume	number of loads (%) with this pollen type	number (%) of pure loads
Boraginaceae	*Pulmonaria*	58.6	35 (67.3)	22 (42.3)
	Symphytum	2.8	4 (7.7)	0 (0)
Fabaceae	*Lathyrus-Vicia*-type	14.8	15 (28.8)	4 (7.7)
	Anthyllis	0.5	1 (1.9)	0 (0)
	Trifolium	0.1	1 (1.9)	0 (0)
	Lotus	0.1	1 (1.9)	0 (0)
	Hippocrepis	0.1	1 (1.9)	0 (0)
	other	2.0	3 (5.8)	0 (0)
Lamiaceae	tricolpate type	13.9	13 (25.0)	0 (0)
	hexacolpate type	0.6	1 (1.9)	0 (0)
Asparagaceae	*Polygonatum*	2.1	3 (5.8)	0 (0)
Rosaceae	*Rubus*	1.9	1 (1.9)	1 (1.9)
Caprifoliaceae	*Lonicera*	0.8	1 (1.9)	0 (0)
Asteraceae	*Taraxacum*	0.3	2 (3.8)	0 (0)
Violaceae	*Viola*	0.2	1 (1.9)	0 (0)
unknown		1.2	2 (3.8)	1 (1.9)

pollen was tricolpate pollen of Lamiaceae represented by 13.9% of the total pollen grain volume and recorded in 13 (25.0%) loads. At our study sites, representatives of all these three main hosts were exploited by females of *O. pilicornis* for pollen, i.e. three *Pulmonaria* species (*P. mollis*, *P. obscura* and *P. officinalis*), *Lathyrus vernus* (Linné) Bernhardi as well as *Ajuga reptans* Linné and *Lamium purpureum* Linné. In addition, pollen harvesting was also ascertained at the flowers of *Glechoma hederacea* Linné, a Lamiaceae species with hexacolpate pollen grains.

Female flower-visiting behaviour

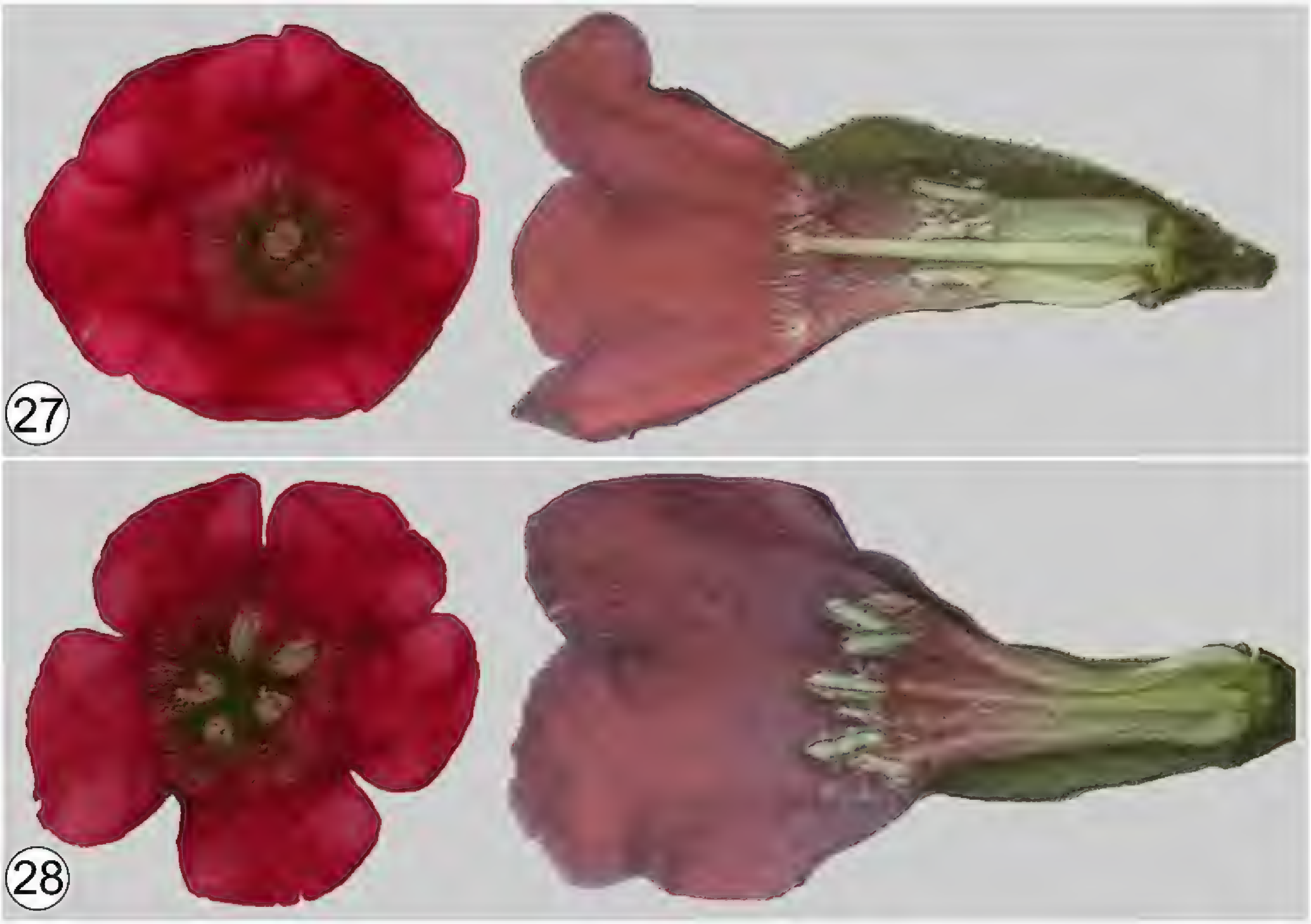
Females of *Osmia pilicornis* used the specialized brush of hooked bristles on their proboscis to remove pollen from the narrow *Pulmonaria* corolla tubes (Fig. 34). Although the action of the mouthparts could not directly be seen as flower-visiting females pressed their head tightly against the small tube entrance, distinct back and forth movements of head and body during flower visitation as well as the conspicuous white coloured *Pulmonaria* pollen that stuck to the black mouthparts after the females had withdrawn them from the flower clearly indicate that the flowers of both the longistylous and the brevistylous morph were brushed out with the aid of the bristled proboscis (Suppl. material 5). Careful examination of video sequences revealed that females removed the pollen from the proboscis in flight with the forelegs immediately after having left the flower (Fig. 33). Flower visits to brevistylous flowers resulted in substantial amounts of pollen sticking to the lower half of the face, suggesting that both the bristled proboscis and the facial pilosity were involved in pollen collection from this flower morph (Fig. 32). Pollen collection on flowers of Lamiaceae also involved the facial pilosity. Females visiting flowers of *Ajuga reptans* and *Glechoma hederacea* pressed their forehead against the anthers while head and body performed rapid up and down movements, which led the pollen to pass over from the anthers to the facial pilosity (Fig. 35, Suppl. material 6). Pollen was removed from the facial pilosity again by stroking movements of the forelegs.

Of a total of 478 flower visits by *Osmia pilicornis* females on *Pulmonaria mollis*, 458 were on red and 20 on blue flowers, revealing a distinct preference of the female bees for the earlier red flower stage (chi-square goodness-of-fit test, χ^2=435.6 df=1, p<0.001; Figs 29, 30). 10.9% of the 458 red flowers visited by the female bees were still in the late bud stage. Here, the females forcefully opened the closed flowers with the aid of head and mouthparts before they harvested pollen and nectar (Fig. 31). The same behaviour could also be observed in several females exploiting flowers of *P. obscura* and *P. officinalis*. Bud-exploiting females were repeatedly observed to visit the same bud twice or three times in direct succession only interrupted by a short hovering flight in front of the bud. This suggests that the loading capacity of the pollen-harvesting bristles of the proboscis was not sufficient to completely empty the flower bud with a single visit, but that the females had first to remove the pollen sticking to their proboscis before landing again to harvest the remaining pollen.

Flowers of *Pulmonaria mollis* in the red stage contained on average 1.65 µl nectar per flower, which did not significantly differ from the quantity of nectar in flowers of the blue stage averaging 2.06 µl per flower (Mann-Whitney U test, U=531.0, p=0.86, n=33 red and blue flowers each). The filling degree of the anthers with pollen (measured as average degree of thecal pollen coverage, see Methods) was 64% in red and 8% in blue flowers of *P. obscura* and 67% in red and 9% in blue flowers of *P. officinalis*, revealing a substantial difference in the pollen quantity available in the two flower stages (Mann-Whitney U tests, U=6.5 and U=17.5, p<0.001, n=20 red and blue flowers each for both species). In 3 out of 20 *P. officinalis* flowers opened in the late bud stage all five anthers were still closed, whereas in 12 buds all anthers and in 5 buds part of the anthers had dehisced, indicating that most flowers in the late bud stage can already be exploited for pollen.

Females of *Osmia pilicornis* exploited both longistylous and brevistylous flowers (Figs 27, 28). During the first observation period (see Methods), they exhibited a preference for brevistylous flowers (chi-square goodness-of-fit test, χ^2=14.7 df=1, p<0.001), while no difference in the proportion of visits to longistylous and brevistylous flowers was found during the second observation period (chi-square goodness-of-fit test, χ^2=0.65, df=1, p=0.42).

Females of *Osmia pilicornis* regularly interrupted their foraging on *Pulmonaria mollis* to land on the ground for short periods varying in duration from 15 to 270 sec. During these resting periods, the mouthparts were constantly moved back and forth (Fig. 36, Suppl. material 7). Careful examination of video sequences revealed droplets

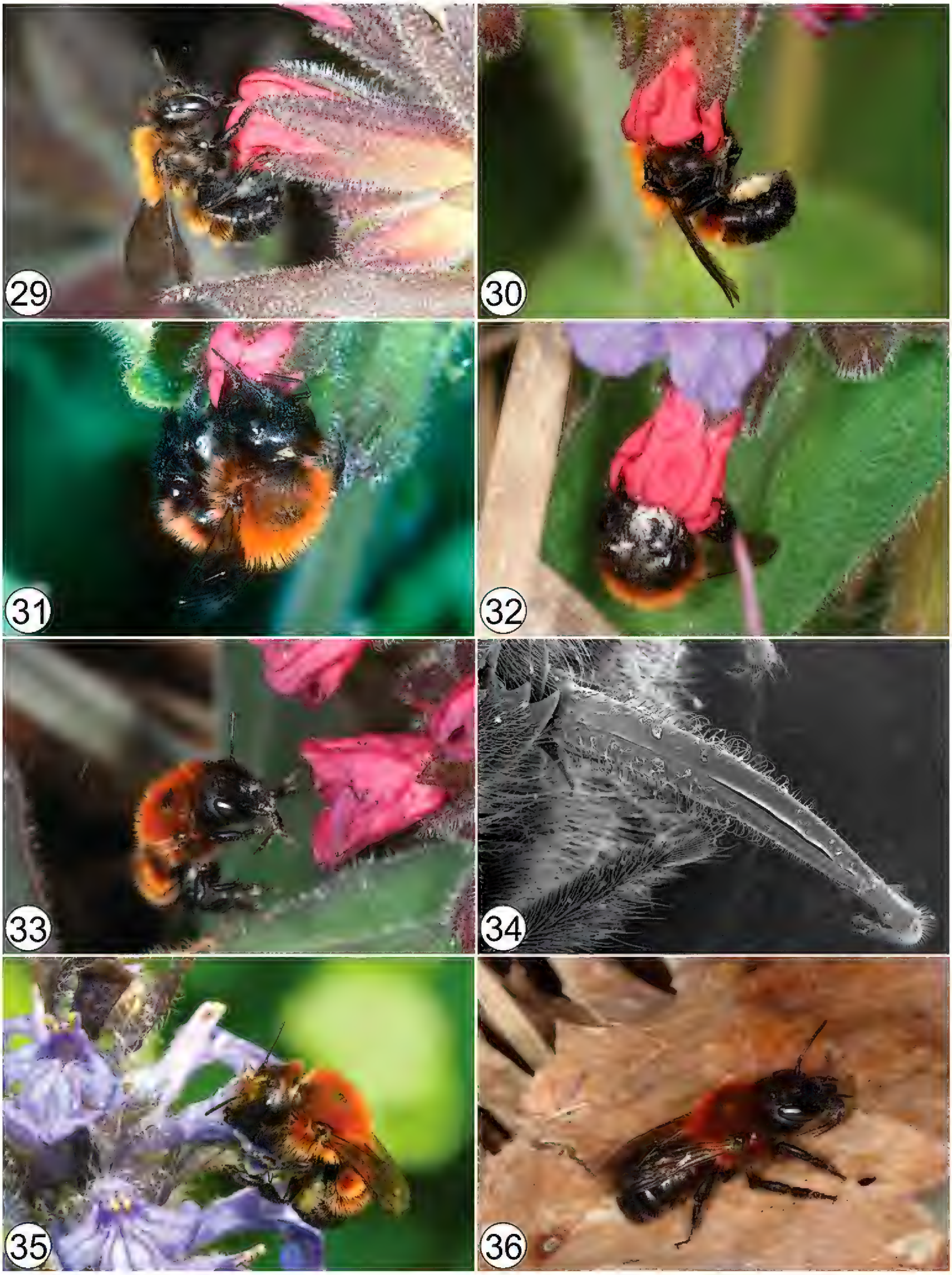


Figures 27–28. Floral morphs of *Pulmonaria mollis* in top and lateral view: **27** Longistylous flower with anthers deeply hidden within the floral tube **28** Brevistylous flower with anthers located at the entrance of the floral tube.

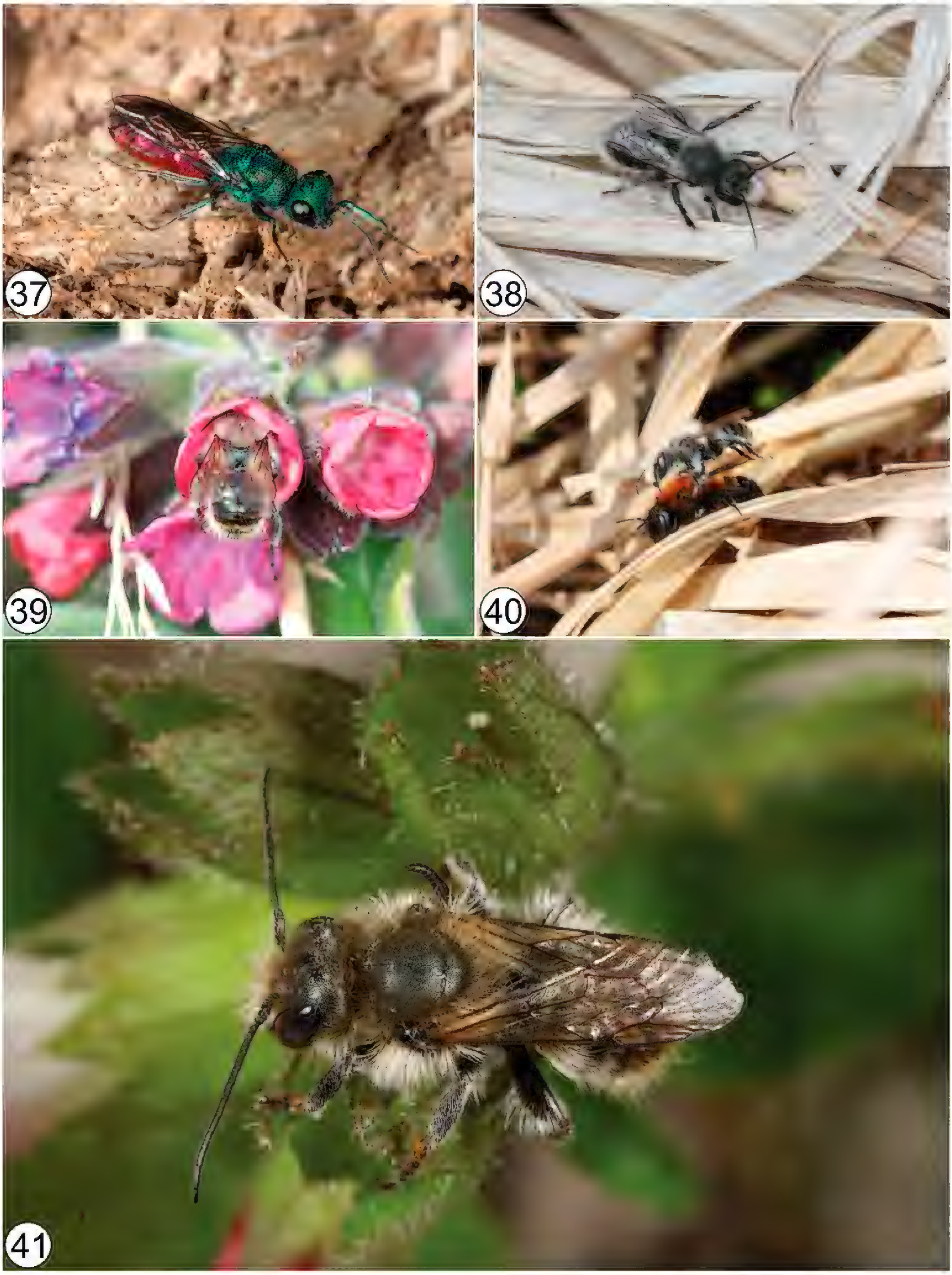
of a fluid on the mouthparts, suggesting that this behaviour served to thicken the collected nectar.

Male mating strategy

On their search for females, males of *Osmia pilicornis* patrolled flowers of *Pulmonaria* in a rapid flight, which was regularly interrupted by short resting periods at sunny spots on or near the ground, such as fallen leaves, flexed grass blades or tree stumps (Fig. 38). These resting periods lasted from 10 to 40 sec. In one case a male returned to his resting place every 5-7 min at least ten times in succession, which suggests that this male patrolled along a more or less fixed circular route. The males occasionally discontinued their patrolling flights to suck nectar on flowers of *Pulmonaria* (Fig. 39). Males were never observed to search for females at or near nests, suggesting that (potential) nesting sites do not serve as rendezvous places for the two sexes. Three copulations were observed: in two cases the male grabbed the female during her visit to a *Pulmonaria* flower, in another case the male grasped the female in flight immediately after she had left a *Pulmonaria* flower. In all three cases the pair fell on the ground, where the copulation was completed within 50 to 80 sec (Fig. 40).



Figures 29–36. Flower-visiting behaviour of *Osmia pilicornis*: **29–30** Females collecting pollen on flowers of *Pulmonaria mollis* in the early red stage **31** Female forcefully opening a bud of *Pulmonaria obscura* **32** Female collecting pollen on brevistylous flower of *Pulmonaria mollis* **33** Female removing pollen sticking to the bristled proboscis with her forelegs **34** Specialized pollen-harvesting bristles on the galeae of the female proboscis **35** Female collecting pollen on flower of *Ajuga reptans* **36** Female moving her proboscis back and forth, thereby probably thickening the collected nectar.



Figures 37–41. Brood parasites and male mating strategy of *Osmia pilicornis*: **37** Female of the chrysidid wasp *Chrysura hirsuta* lurking near nest of *O. pilicornis* **38** Male resting on flexed grass blades lying on the ground **39** Male sucking nectar on flower of *Pulmonaria mollis* **40** Pair separating after copulation on the ground **41** Male with well visible hairs along the posterior margin of the antennae.

Habitat

During the study period, *Osmia pilicornis* was observed at nine different localities in Germany, Austria and Switzerland. At six further localities, where we recorded the species after 1990, its presence could not be confirmed. All localities including the unconfirmed ones were open-structured, deciduous woodland sites rich in dead wood between 330 and 650 m a.s.l. on rather nutrient-rich soil with a well developed layer of herbaceous spring flowers (Figs 42–47). More specifically, we found the species along forest edges (n=5) and broad forest tracks (n=3), on clear-cuttings and clearings (n=4) and in thinned forests (n=2) and coppiced woodland (n=1).

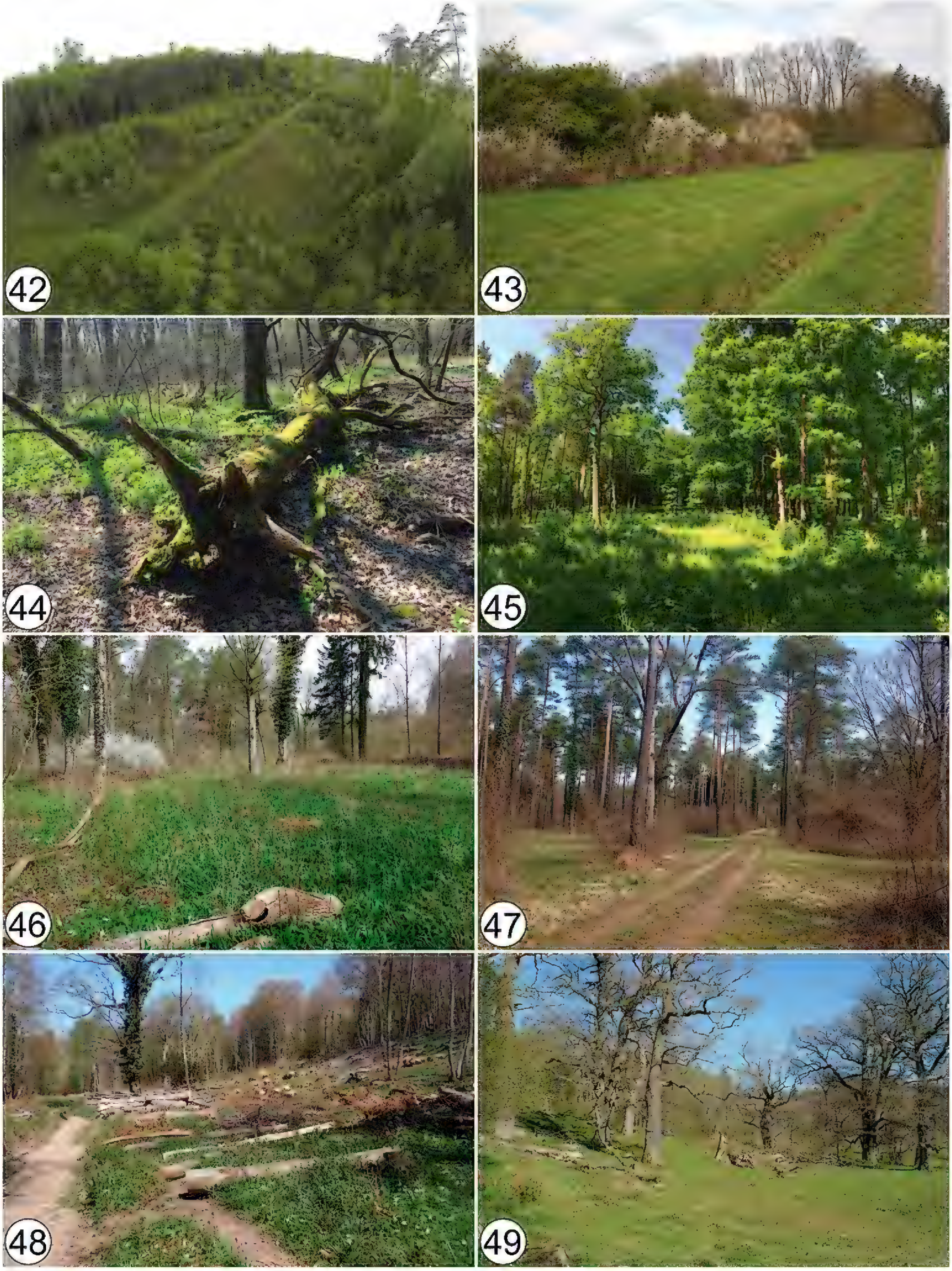
The maximal number of individuals of *Osmia pilicornis* recorded at the same locality and date was three females and two males, while at most localities only one or two individuals were simultaneously observed, indicating very low population densities at the study sites.

Discussion

Nesting biology of *Osmia pilicornis*

Our discovery of six nests at two localities in Germany and Austria built by at least five different bee individuals clearly show that females of *Osmia pilicornis* gnaw their nest burrows in dead wood. Thus, our findings contradict the assumption that *O. pilicornis* constructs its brood cells under loose bark (Amiet et al. 2004) or within preexisting insect borings (Earwaker 2014, Falk and Lewington 2015), but instead confirm observations in Britain from the nineteenth century that *O. pilicornis* burrows in dead wood (Wallis 1886, Perkins 1891). Our findings also explain why the repeated attempts to establish *O. pilicornis* in trap nest composed of drilled borings in dead wood or hollow stems all have failed (R. Earwaker personal communication, R. Prosi and A. Müller unpublished data).

Interestingly, the female mandibular shape of *Osmia pilicornis* differs from that of other *O.* (*Melanosmia*) species. Compared with closely related species that also use leaf pulp as nest building material but exclusively nest in preexisting cavities such as *O. inermis* (Zetterstedt) or *O. parietina* Curtis (Frey-Gessner 1880, Priesner 1981, Westrich 1989, Else and Edwards 1996, Hicks 2009, A. Müller unpublished data), the mandibles of *O. pilicornis* are relatively shorter, more compact and apically less curved resulting in a chisel-like shape that appears to be well suited to tunnel out burrows in dead wood. In addition, the distinctly broader and more inflated mandibular base suggests the presence of strong mandibular muscles, which might provide the needed strength to burrow even in hard wood. We thus hypothesize that the peculiar mandibular shape in females of *O. pilicornis* is an adaptation to the species' specialized nesting behaviour.



Figures 42–49. Habitats of *Osmia pilicornis*: **42** Clear-cutting in southern Germany west of Crailsheim **43** Forest edge in southern Germany northeast of Crailsheim **44** Coppiced woodland in northeastern Austria near Ernstbrunn **45–47** Thinned forests in northeastern Austria near Ernstbrunn (**45**) and in northern Switzerland near Flaach (**46**, **47**) **48** Clear-cutting in southern England near Battle in East Sussex (photo R. Earwaker) **49** Pasture in semi-open, oak-dominated woodland in middle Sweden near Sparreholm in Södermanland (photo A.L. Nilsson).

All six nests were in dead branches, which had a diameter of 1.5–6.1 cm, lay on the ground and were largely hidden under vegetation. A nest found by Chambers (1949) was also in a broken branch and we often observed females that searched for suitable nesting sites flying close to the ground and patrolling 2-10 cm thick branches. Nest-searching females were also repeatedly seen to fly or crawl under vegetation or grass tussocks. Thus, dead branches of moderate diameter lying on the ground and partly hidden by vegetation appear to represent the typical nesting site of *Osmia pilicornis.* The discovery of a nest of *O. pilicornis* in a tree stump by Blüthgen (1919), however, suggests that dead wood other than broken branches might occasionally also serve as nesting site.

The six nests were carved out in dead branches of *Fraxinus excelsior* Linné, *Picea abies* (Linné) Karsten, *Salix* spec. and *Corylus avellana* Linné. The nest detected by Blüthgen (1919) was in a stump of *Fagus sylvatica* Linné and Chambers (1949) assumed the nesting branch he found to probably originate from *Quercus*. The different kinds of wood selected as nesting substrate indicate that *Osmia pilicornis* is flexible in its choice of wood for nesting. A similar flexibility was observed with respect to the direction of the nest entrance and the hardness of the nesting wood. The nest entrances were directed from northeast to south-southwest and both hard and soft wood was used as nesting substrate.

The nests of *Osmia pilicornis* discovered in the course of our study contained only one to three brood cells, which is in line with Chambers (1949), who reported two cells for the nest he discovered. Thus, the construction of few-celled nests appears to be a typical trait of *O. pilicornis*. As females of osmiine bees usually lay up to 20 eggs during their lifetime under natural conditions (Raw 1972, Hawkins 1975, Correia 1981, Haeseler 1982, Müller 1994), a female of *O. pilicornis* is expected to construct a number of nests in several branches during her flight period.

In all nests the main part of the nesting burrow, which harboured the brood cells and ran in longitudinal direction of the branch, deviated from the short entrance part by an angle of 90-140°. This suggests that the females gnawed into the wood until they reached a sufficient depth to continue their tunneling in longitudinal direction, which possibly might have been less labour intensive than gnawing perpendicular to the wood fibers.

We identified leaves of *Fragaria vesca* as material to construct both cell partitions and nest plug. Interestingly, Westrich (2010) observed a female of *Osmia pilicornis* collecting leaf pulp on the same plant species, suggesting that *Fragaria vesca* might play a prominent role as source of nest-building material.

Nesting biology of *Osmia* (*Melanosmia*)

The nesting biology of *Osmia* species of the subgenus *Melanosmia* is diverse (Cane et al. 2007, Müller 2016, and references therein). While the majority of species construct cell partitions, nest plug or entire brood cells with leaf pulp as *O. pilicornis*, others combine leaf pulp with wood fibers, pith, mud, sand grains or small pebbles, or exclusively use mud as nesting material, sometimes under addition of small pebbles. Although information on the nesting sites is available only for about 50 of the 135 *O.* (*Melanosmia*) species (Cane et al. 2007, Müller 2016, and references therein), most species appear to nest in preexisting cavities, such as insect borings in dead wood, hollow stems, holes and fissures in stones and walls, abandoned nests of other aculeates or deserted galls. Others attach their brood cells to the underside of stones, hide them among dense vegetation and litter or excavate their own burrows in the ground. So far, only two *O.* (*Melanosmia*) species are reported to occasionally gnaw burrows in dead wood. The Nearctic *O. bucephala* Cresson was observed to tunnel out burrows in a maple tree (Packard 1868) and the Holarctic *O. nigriventris* (Zetterstedt) was found to nest in burrows in bark and decaying wood, which were at least partly excavated by the female bees (Frey-Gessner 1881, Friese 1911, Amiet et al. 2004). However, at least the former species also colonizes preexisting burrows in dead wood or trap nests (Krombein 1967, Sheffield et al. 2003), suggesting a considerable intraspecific flexibility in nest site selection. To the best of our knowledge, excavation of burrows in dead wood is unknown in osmiine bees other than *Melanosmia*. Thus, the nesting behaviour of *O. pilicornis*, which constructs its brood cells most probably exclusively in self excavated burrows in dead wood, appears to be unique among both *Melanosmia* and the Osmiini, contributing a further facet to the astonishingly diverse nesting biology of the osmiine bees.

Brood parasites

No brood parasites have been recorded for *Osmia pilicornis* so far. However, Blüthgen (1919) found larvae of *Meloe* beetles (Meloidae) adhering to the body of several specimens of *O. pilicornis* as we did in the present study, suggesting that these parasitic beetles might occasionally develop in nests of *O. pilicornis*. However, as osmiine bees have never been recorded as hosts of Central European *Meloe* species (Lückmann and Niehuis 2009), the beetle larvae might have used *O. pilicornis* simply for dispersal.

Our observation of *Chrysura hirsuta* approaching, entering or flying in close neighbourhood of nests of *Osmia pilicornis* as well as the discovery of a dead chrysidid wasp larva inside a brood cell of nest 2 clearly reveals that *O. pilicornis* is a host of this chrysidid wasp species. *Chrysura* species are metaparasitoids of osmiine bees (Krombein 1967, Morgan 1984, Kunz 1989). After eclosion, their larvae attach to the body of the feeding bee larva with their mandibles and start devouring its host only after the latter has eaten the entire food provision and spun a cocoon. In the literature, several osmiine bee species are mentioned as hosts of *C. hirsuta*. However, not all of these records seem to be reliable as they are either based on personal communication rather than direct observation by the authors, are not detailed enough to judge their reliability or rely on the mere coocurrence of wasp and bee at the same place. Three osmiine bee species are confirmed hosts since *C. hirsuta* has been reared from their nests: *Hoplitis*

(*Alcidamea*) *tuberculata* (Nylander) (Trautmann 1918), *Osmia* (*Melanosmia*) *inermis* (Zetterstedt) (Xambeu in Buysson 1891, Evans 1896 as *Osmia parietina*, Maneval in Berland and Bernard 1938, Morgan 1984, Falk and Lewington 2015) and *Osmia* (*Melanosmia*) *xanthomelana* (Kirby) (Trautmann 1918, Enslin 1920). Given their close relatedness with some of the above hosts and their main occurrence in mountainous or northern regions where *C. hirsuta* has its main distribution (Kunz 1989), the following species are probably also hosts of *C. hirsuta*, although no proof for the wasp's development within their nests exists: *Osmia* (*Melanosmia*) *nigriventris* (Zetterstedt) (Zetterstedt in Berland and Bernard 1938, Trautmann 1927, Stoeckhert 1933, Paukkunen et al. 2014), *Osmia* (*Melanosmia*) *parietina* Curtis (Smith in Trautmann 1927, Dalla Torre in Berland and Bernard 1938, Falk and Lewington 2015) and *Osmia* (*Melanosmia*) *uncinata* Gerstäcker (Forsius in Trautmann 1927, Falk and Lewington 2015). Possible further hosts are *Hoplitis* (*Anthocopa*) *villosa* (Schenck) (Maneval in Berland and Bernard 1938), *Osmia* (*Helicosmia*) *aurulenta* (Panzer) (Benoist in Berland and Bernard 1938) and *Osmia* (*Metallinella*) *brevicornis* (Fabricius) (Trautmann 1927). Although the authors report that *C. hirsuta* has been reared from nests of these latter three species, the evidence is ambiguous as these records are either not based on direct observation by the authors or lack necessary additional information. *Chelostoma florisomne* (Linné) was also supposed to be a host of *C. hirsuta* (Berland and Bernard 1938) as the chrysidid wasp was observed to fly in the vicinity of its nests in dead wood (Frey-Gessner 1887). However, as *H. tuberculata* nested in the same dead wood as *C. florisomne* according to the author, *C. hirsuta* probably parasitized the former species. In summary, the above list of confirmed, probable and possible hosts includes numerous *Melanosmia* species, suggesting that species of this subgenus are the main hosts of *C. hirsuta*. Our new finding that *C. hirsuta* also attacks the nests of *O. pilicornis* supports this assumption.

In four brood cells of *Osmia pilicornis* in nest 1 and 2 the ichneumonid wasp *Hoplocryptus confector* developed. Hosts of this parasitoid wasp are mainly stem-nesting aculeate hymenopterans (Schwarz 2007 and references therein). As the wasp is known to parasitize species of both osmiine bees and chrysidid wasps, it remains unclear whether *O. pilicornis* served as host or whether the wasps developed as hyperparasitoids on the larvae of *Chrysura hirsuta*.

Host plants

Pollen hosts

In this study, *Pulmonaria* (Boraginaceae) was identified as the most important pollen host of *Osmia pilicornis* in Central Europe, supporting earlier findings by other authors (Stoeckhert 1933, Westrich 1989, Müller 1995, Amiet et al. 2004, Ebmer 2010). *Pulmonaria* is also an important pollen source of *O. pilicornis* outside Central Europe (Arnold 1902, Benoist 1931, Moczar 1956, Papp 1965, Kuznetsova 1990, T.

Levchenko and L.A. Nilsson personal communication) and might therefore be considered as the species' main host across most of its range. This assumption is supported by the presence of a specialized morphological adaptation facilitating the exploitation of *Pulmonaria* flowers, i.e. numerous hooked bristles on the female proboscis, which are specifically used to brush pollen out of the narrow *Pulmonaria* corolla tubes (Müller 1995, this study). Interestingly, *Pulmonaria* is lacking on the British Isles and British populations of *O. pilicornis* primarily rely on the pollen of two Lamiaceae species, i.e. *Ajuga reptans* and *Glechoma hederacea* (Chambers 1949, Beavis 2010, Earwaker 2014, Falk and Lewington 2015). Here, the specialized pollen-harvesting bristles seem to be without any function. As the phenologies of *Pulmonaria* and *O. pilicornis* are not fully congruent in continental Europe, where the flowering period of *Pulmonaria* usually covers only about the first half of the bee's flight period, females of *O. pilicornis* have to exploit other pollen hosts later in the season. This again clearly indicates that *O. pilicornis* is not entirely dependent on *Pulmonaria* and that its populations might thrive also in the absence of the species' main host. Nevertheless, the Central European populations of *O. pilicornis* seem to be linked to localities with large *Pulmonaria* stands, which suggests that the efficient harvesting of *Pulmonaria* pollen in early spring facilitated by the specialized pollen harvesting device may provide a substantial advantage that might tie the bee to *Pulmonaria*. On the other hand, the apparently exclusive occurrence of *O. pilicornis* at localities where *Pulmonaria* is present might be an artefact since bee researchers use to search for this rare bee species at places with large *Pulmonaria* stands. In fact, in Sweden populations of *O. pilicornis* exist at localities where *Pulmonaria* is absent (L.A. Nilsson and L. Norén personal communication). To date, the question must remain open whether Central European populations of *O. pilicornis* only occur at places with *Pulmonaria* stands or whether this rare bee has simply been overlooked at *Pulmonaria* free woodland sites.

Major pollen hosts of *Osmia pilicornis* other than *Pulmonaria* are several species of Fabaceae and Lamiaceae. The analysis of female pollen loads (Table 3) in combination with literature records and personal communication from bee researchers reveals that the most important pollen host genera of European populations of *O. pilicornis* are among the Fabaceae *Lathyrus* (Stoeckhert 1933, Westrich 1989, T. Levchenko and L.A. Nilsson personal communication) and *Vicia* (Westrich 1989, T. Levchenko personal communication) and among the Lamiaceae *Ajuga* (Stoeckhert 1933, Chambers 1949, Westrich 1989, Beavis 2010, Earwaker 2014, Falk and Lewington 2015, this study) and *Glechoma* (Earwaker 2014, this study). Additional albeit apparently only secondary pollen host genera of the Fabaceae are *Anthyllis* (Table 3), *Hippocrepis* (Stoeckhert 1933, Westrich 1989, Table 3), *Lotus* (Table 3) and *Trifolium* (T. Levchenko personal communication, Table 3) and of the Lamiaceae *Lamium* (this study) and *Salvia* (Westrich 1989). Pollen of other plant taxa seems to have only a minor significance for *O. pilicornis*. Confirmed pollen sources other than *Pulmonaria* and species of Fabaceae and Lamiaceae are *Lonicera* (Caprifoliaceae; Table 3), *Polygonatum* (Asparagaceae; Benoist 1931, Table 3), *Potentilla* (Rosaceae; Westrich 1989), *Rubus* (Rosaceae; L.A. Nilsson personal communication, Table 3), *Symphytum* (Boraginaceae; L.A. Nilsson personal communication, Table 3), *Taraxacum* (Asteraceae; Table 3) and *Viola* (Violaceae; Wallis 1886, Friese 1911, Benoist 1931, Chambers 1949, Elfving 1968, Table 3). Most of these latter pollen host genera occur at woodland sites reflecting the bee's exclusive habitat.

Female flower-visiting behaviour

Flower visiting females of *Osmia pilicornis* exhibited a distinct preference for *Pulmonaria* flowers in the earlier red stage and only occasionally visited flowers in the later blue stage. As both stages were found to offer nectar in similar quantities, the near exclusive exploitation of flowers in the red stage is most likely due to differences in the amount of pollen. In fact, flowers in the red stage contained much more pollen than flowers in the blue stage, which were usually almost devoid of pollen due to their older age and the putatively higher number of flower visits they already had experienced. The forceful opening of *Pulmonaria* flower buds seems to be a regular behaviour as it could be observed in numerous females exploiting three different *Pulmonaria* species at three localities. Undoubtedly, this behaviour is highly adaptive as it enables the females to collect large quantities of pollen within a short period of time.

Our results on the proportion of longistylous and brevistylous flowers visited by females of *Osmia pilicornis* are ambiguous. The females preferred brevistylous over longistylous flowers during the first observation period, but exhibited no preference for one of the two floral morphs during the second observation period. We hypothesize that this incongruency might possibly be due to *Anthophora plumipes*, which was common at the study site during the first but entirely lacked during the second observation period. Like *O. pilicornis*, females of *A. plumipes* are morphologically adapted to remove pollen out of the narrow *Pulmonaria* flower tubes (Müller 1995). Since *O. pilicornis* and *A. plumipes* are among the few flower visitors that can efficiently exploit longistylous flowers for their deeply hidden pollen, longistylous flowers should be more attractive to these two species due to their higher standing crop of pollen compared to brevistylous flowers, which can be exploited for pollen by a larger proportion of flower visitors. Thus, the numerous females of *A. plumipes* that visited the *Pulmonaria* flowers earlier in the season might possibly have preferentially emptied longistylous flowers, thereby indirectly forcing the few females of *O. pilicornis* to exploit a larger proportion of brevistylous flowers. Later in the season, when *A. plumipes* was no longer present, a higher proportion of unemptied longistylous flowers was available for *O. pilicornis* resulting in a more balanced visitation rate of longistylous and brevistylous flowers.

Females of *Osmia pilicornis* collected pollen on nototribic flowers of the Lamiaceae with the aid of their facial pilosity. In contrast to numerous other bee species, which are equipped with a specialized pollen-collecting apparatus on clypeus and/or frons to harvest pollen on nototribic flowers (Müller 1996, Rightmyer et al. 2011), the facial hairs of *O. pilicornis* are not specialized and correspond in length, density and shape to those of other *O.* (*Melanosmia*) species, such as *O. inermis* or *O. parietina*, which do not harvest pollen from Lamiaceae but instead exploit mainly Fabaceae (Westrich 1989, Müller 2016).

In summary, females of *Osmia pilicornis* are highly adapted to efficiently collect pollen in several respects. On flowers of *Pulmonaria*, they use specialized bristles on the proboscis to brush pollen out of the corolla tubes, they almost exclusively exploit pollen-rich flowers in the red stage and they often steal pollen from still closed flowers by forcefully opening buds. On flowers of Lamiaceae, they remove pollen from the nototribic flowers by applying a specialized behaviour that involves the facial pilosity.

Male mating strategy

Although still only fragmentarily known, the mating strategy of the males of *Osmia pilicornis* seems to correspond to that of other osmiine bee species, such as *Hoplitis zandeni* (Teunissen and Van Achterberg) or *Osmia spinulosa* (Kirby). In these two species, both of which nest in empty snail shells (Müller 1994, Müller and Mauss 2016), the males also patrol flowers of the female host plants in a fast flight along more or less fixed circular routes regularly interrupted by short resting periods on the ground. As in *O. pilicornis*, they do not search for females at potential nesting sites, probably since the habitat of the former species contains huge numbers of empty snail shells making nest localization difficult and the females of the latter species exhibit strict pollen specialization making female detection straightforward. A similar discrepancy in the probability of finding females at *Pulmonaria* flowers and the widely scattered and inconspicuous nesting sites, respectively, might be the reason why flowers seem to serve as exclusive rendezvous places for the two sexes of *O. pilicornis*. In fact, the amount of dead fallen branches was often large in habitats occupied by *O. pilicornis* making it almost impossible for the males to localize nests. As the males of *O. pilicornis* were not observed to defend their flight routes against conspecifics as for example in *O.* (*Melanosmia*) *maritima* Friese (Haeseler 1982), their mating strategy might be best described as scramble competition polygyny (Thornhill and Alcock 1983).

The males of *Osmia pilicornis* are characterized by numerous long hairs along the entire posterior margin of their antennae (Fig. 41). The function of this specialized pilosity, which is unique among osmiine bees and gave *O. "pilicornis"* its species epithet, is unknown. As these hairs are absent in the female sex, they might possibly help in the perception of the females or play a role during copulation or courtship.

Habitat

Our observations confirm other authors, who assume *Osmia pilicornis* to be strongly restricted to woodland habitats (Stoeckhert 1933, Westrich 1989, Amiet et al. 2004, Falk and Lewington 2015). This clear habitat preference, which appears to be valid across the species' entire range (Figs 48, 49), may primarily be explained by the need for dead fallen branches as nesting sites. *O. pilicornis* never colonizes closed and dark forests but instead exhibits an exclusive preference for semi-open, sunny, rather warm and deciduous woodland habitats rich in dead wood below 1000 m a.s.l. The fact that the species usually colonizes mesophilous rather than xeric woodland is probably due to its need of a rich supply of pollen hosts flowering in early spring, which requires nutrient-rich edaphic conditions. The spectrum of open-structured woodland types colonized by *O. pilicornis* is surprisingly wide and ranges from clearings and clear-cuttings over forest edges and forest tracks to thinned and coppiced woodland, suggesting that dead fallen branches and a rich spring flora in combination with a rather warm microclimate are the only requisites needed by the species. Interestingly, the majority of woodland habitats currently colonized by *O. pilicornis* in Central Europe owe their origin to human forest use. This raises the question about the primary habitats of the species in Europe in prehistoric times. We hypothesize that the primary habitats of *O. pilicornis* were either windfalls or woodland sites kept open by the former grazing megafauna (A. Nilsson personal communication, Bunzel-Drüke et al. 2008).

Populations of *Osmia pilicornis* at our study sites were remarkably small and often contained only single individuals. Such low population densities seem to be typical for *O. pilicornis* throughout its range. Of 516 records of *O. pilicornis* that could be assigned an exact date and contained information on individual numbers (see list of all distributional data in the Suppl. material 1), 91.1% had 1-2 individuals, 7.7% 3-5 individuals and 1.2% 6-11 individuals recorded at the same locality and date. The highest number of females simultaneously observed at the same site was 7 and the highest number of males was 10. These overall very low population densities are probably not due to food limitation as *Pulmonaria* often occurs in large stands and *O. pilicornis* is able to collect pollen from a variety of plant taxa. Nor do they seem to be explained by special characteristics of the wood used for nesting as *O. pilicornis* was found to nest in dead branches of different species and of varying hardness. Instead, we hypothesize that a high pressure by brood parasites might possibly be an important reason contributing to the low population densities. In fact, five out of the six brood cells of nests 1-3 were found to be parasitized. A high brood-parasite pressure would also explain why the females of *O. pilicornis* construct nests that contain only few brood cells, thereby possibly reducing the risk to loose all progeny after a brood parasite has detected a nest.

Conservation

Populations of *Osmia pilicornis* have regressed in many regions of Europe over the last decades resulting in the species' inclusion in numerous regional or national red lists (Amiet 1994, Winter 1994, Dathe and Saure 2000, Saure 2005, Westrich et al. 2000, 2008, Van der Smissen 2001, Theunert 2002, Mandery et al. 2003, Burger et al. 2004, Burger 2005, Straka 2005, Tischendorf et al. 2009, Esser et al. 2010, Earwaker 2012). In our study, *O. pilicornis* was no longer found at six out of 15 localities, although the former were still colonized 3-25 years ago, supporting its status as a declining and threatened species. Although this recent decline is poorly understood, changes in woodland management practices might be an important reason, in particular the abandonment of the area-wide but little intensive former human forest use, which led to the closed and dark forests now prevailing in most regions of Central Europe at lower elevations. Due to the species' overall rareness and low population densities, its widely scattered and often highly localized occurrence and the reported recent declines, current Central European populations of *O. pilicornis* need regular monitoring and deserve protection. Measures to conserve and foster *O. pilicornis* should focus on the preservation of the semi-open structure and the rich supply of dead wood in currently colonized woodland habitats as well as the new creation of such habitats by thinning or clearing of woodland on nutrient-rich soils at warm but not xeric sites, preferentially in close neighbourhood to existing populations of *O. pilicornis*.

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Supplementary material 1

List of distributional data of *Osmia pilicornis*

Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller

Data type: distributional data

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Supplementary material 2

Female of *Osmia pilicornis* gnawing nesting burrow

Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller

Data type: species data

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Supplementary material 3

Female of *Osmia pilicornis* provisioning brood cell

Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller

Data type: species data

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Supplementary material 4

Female of *Osmia pilicornis* constructing nest plug

Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller

Data type: species data

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Supplementary material 5

Female of *Osmia pilicornis* collecting pollen on *Pulmonaria mollis*

Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller

Data type: species data

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Supplementary material 6

Female of *Osmia pilicornis* collecting pollen on *Ajuga reptans*
Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller
Data type: species data
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Supplementary material 7

Female of *Osmia pilicornis* thickening nectar
Authors: Rainer Prosi, Heinz Wiesbauer, Andreas Müller
Data type: species data
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